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Published in:
Acta Protozoologica

DOI:
[10.4467/16890027AP.14.006.1443](https://doi.org/10.4467/16890027AP.14.006.1443)

Publication date:
2014

Document version
Early version, also known as pre-print

Citation for published version (APA):
Skovgaard, A. (2014). Dirty tricks in the plankton: Diversity and Role of Marine Parasitic Protists: diversity and role of marine parasitic protists. *Acta Protozoologica*, 53(1), 51-62.
<https://doi.org/10.4467/16890027AP.14.006.1443>

Special issue:

Marine Heterotrophic Protists

Guest editors: John R. Dolan and David J. S. Montagnes

Review paper

Dirty Tricks in the Plankton: Diversity and Role of Marine Parasitic Protists

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Abstract. Parasitism is an immensely successful mode of nutrition and parasitic organisms are abundant in most ecosystems. This is also the case for marine planktonic ecosystems in which a large variety of parasitic species are known. Most of these parasites are protists and they infect a wide range of hosts from the marine plankton, ranging from other protists to larger planktonic invertebrates. Parasites often have morphologies and life cycles that are highly specialized as compared to their free-living relatives. However, this does not mean that parasites are necessarily odd or rare phenomena; on the contrary parasites constitute numerically and ecologically important components of the ecosystem. This review gives an overview of the existing knowledge on the diversity and occurrence of parasitic protists in the marine plankton and examines the available information on the potential effects and role of parasitism in this ecosystem. Importance is given to the fact that prevalence and impact of parasitic organisms in marine planktonic systems appear to be overwhelmingly understudied.

Key words: Parasite, parasitoid, phytoplankton, plankton, zooplankton.

INTRODUCTION

Early studies on energy transfer between components of the marine plankton tended to consider the route of energy transfer as a relatively simple food chain in which organic matter is transferred from photoautotrophic phytoplankton to larger heterotrophic zooplankton and onwards to higher trophic levels (e.g. Steele 1970). However, in the late 20th century, an awareness has appeared that energy transfer between trophic levels in

the marine plankton occurs through a highly complex food web. For example, phytoplankton cells leak a substantial amount of organic carbon fixed through photosynthesis, by which primary production is exploited by bacteria rather than by eukaryotic grazers (e.g. Azam *et al.* 1983). Furthermore, the traditional perception that plankton predators are typically an order of magnitude larger than their prey (e.g. Sheldon *et al.* 1977) has turned out not to be a general rule. On the contrary, some of the dominating microeukaryotic predators, the dinoflagellates, feed on prey cells of approximately their own size (Hansen *et al.* 1994). When a protist cell feeds on a prey larger than itself, the feeding strategy can in many cases be characterized as parasitism.

Parasitism in general is considered the most common consumer strategy in nature and it may be argued

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that roughly half of the species on Earth are parasites (Windsor 1998, de Meeûs and Renaud 2002). On the ecosystem level parasites have substantial biomasses that may exceed the biomass of top predators in aquatic ecosystems (Kuris *et al.* 2008). It is, therefore, not surprising that parasitism is also very common among the different components of the marine plankton (Théodoridès 1989, Park *et al.* 2004, Skovgaard and Saiz 2006). Current evidence does not fully justify that parasitism needs to be taken into account when attempting to understand the marine planktonic food web. However, as discussed below, it is probable that only a minority of parasites of planktonic hosts has been identified so far and that parasitism is severely underestimated in current perception of the marine planktonic ecosystem.

Few studies have addressed the ecological importance of parasitism in the marine plankton, which is in contrast to large research efforts dedicated to the function and evolutionary ecology of plankton parasitology in freshwater phytoplankton (Kagami *et al.* 2007, Rasconi *et al.* 2012) and zooplankton (Burns 1989, Decaestecker *et al.* 2005, Ebert 2008). In the following it is attempted to highlight the immense diversity of known protistan parasites (including parasitoids and parasitic castrators) in the marine plankton and to expose the current vast lack of knowledge about some of these microbial pathogens.

DIVERSITY OF PARASITES IN MARINE PLANKTON

In the following, the term protist is used as a popular term as suggested by Adl *et al.* (2005), including thus such unicellular eukaryotes as fungi (i.e. uniflagellated Ophisthokonta) and amoebae, which have not traditionally been included in the taxon Protista (Adl *et al.* 2005). A parasite may be defined as an organism utilizing a host as habitat on which it is nutritionally dependent and, furthermore, it causes harm to the host (Anderson and May 1978). This definition thus excludes protists living as epibiotic symbionts on marine plankton, e.g. diatoms and apostome ciliates on copepods (Hiromi *et al.* 1985, Grimes and Bradbury 1992). However, it is acknowledged that the distinction between a symbiotic and a parasitic protist (and even a parasitic and a predatory protist) may not always be feasible and that more specific definitions may be required (Gaines and Elbrächter 1987). Parasitic consumer strategies are found

to various degrees in many protist groups and the diversity of these parasites is exemplified by the following examples of the most characteristic species.

Fungi

True fungi are abundant in the marine environment, but only relatively few species are known to infect plankton organisms and knowledge on the biological interactions and effects of fungal infections in marine plankton is still limited. A few examples are known among the Chytridiomycetes, such as *Olpidium* and *Rhizophyidium*, that able to infect the marine diatoms *Pseudo-nitzschia* and *Chaetoceros* (Elbrächter and Schnepf 1998, Wang and Johnson 2009). In addition to the true fungi, several species of aquatic 'fungi' of the Stramenopiles are known from marine phytoplankton (see below).

Amoebozoa

Amoeba biddulphiae was described almost a century ago from the marine diatom *Odontella (Biddulphia) sinensis* (Fig. 1A, Zuelzer 1927). Another amoeba, *Rhizamoeba schnepfii* (Tubulinea, Adl *et al.* 2005), also infects and feeds on marine diatoms, but unlike *A. biddulphiae*, it is able to exploit a suite of diatom species (Kühn 1997a). *Pseudophelidium schnepfii* (Mesomyxozoa, Adl *et al.* 2005) is a parasite of the centric marine diatom *Thalassiosira punctigera* (Schweikert and Schnepf 1996) and the amoeba *Janickina* spp. are endoparasites in chaetognates (Weinstein 1973).

Rhizaria

Several distantly related rhizarian species are parasites of plankton organisms, in particular marine diatoms. Among these are species of the cercozoan genera *Cryothecomonas* (Drebes *et al.* 1996) and *Pseudopirsonia*. Originally considered a stramenopile, *Pseudopirsonia mucosa* has proven a member of Cercozoa. *P. mucosa* infects marine diatoms of the genus *Rhizosolenia* in manner much similar to *Pirsonia* (Stramenopiles, Kühn *et al.* 1996). Also other rhizaria, such as *Phagomyxa* spp. are parasites in diatoms (Schnepf *et al.* 2000).

The paramyxan parasite *Marteilia refringens* is a parasite in European flat oyster, *Ostrea edulis*, (Berthe *et al.* 1998), but the presence of *M. refringens* in planktonic copepods suggests that it utilizes copepods as intermediate or transport host (Audemard *et al.* 2002). Carrasco *et al.* (2008) confirmed these findings and demonstrated that *M. refringens* is able to proliferate in copepods, but thus far the possible effect of *P. refringens* on its copepod host remains unknown.

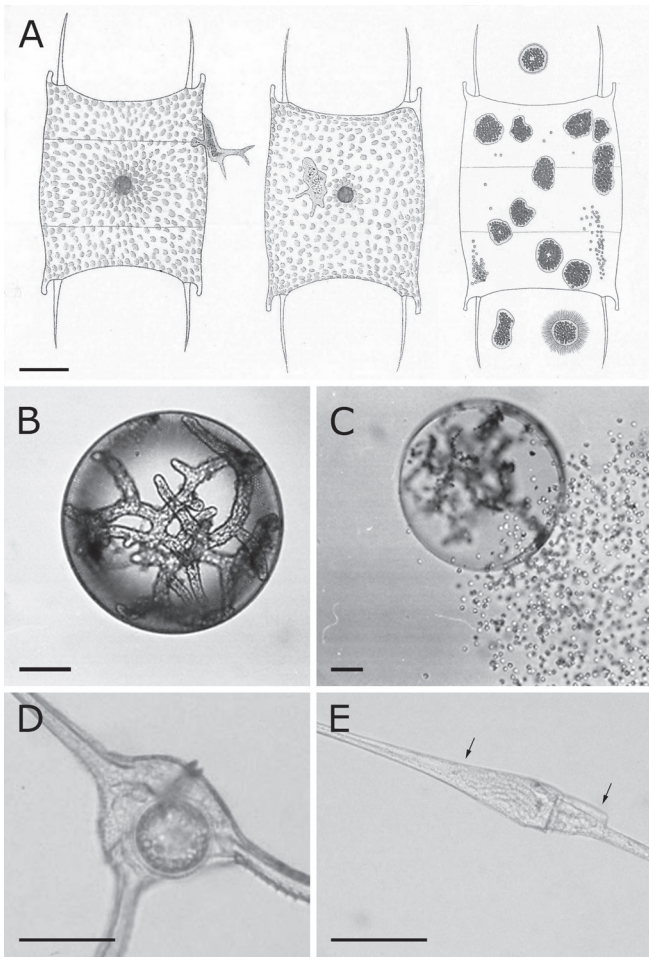


Fig. 1A–E. Protistan parasites of marine phytoplankton. **A** – *Amoeba biddulphiae* in the diatom *Odontella sinensis*. Left: recently attached parasite cell. Center: parasitic amoeba inside the host. Right: almost empty diatom frustule with protoplasm transformed into 10 amoebae (after Zuelzer 1927); **B**, **C** – the stramenopile fungi *Lagenisma coscinodisci* in the diatom *Coscinodiscus* sp.; **B** – host cell protoplasm transformed into parasite hyphae; **C** – expulsion of parasite swarmer cells. Courtesy of Gerhard Drebes, Plankton*Net Data Provider at the Alfred Wegener Institute for Polar and Marine, <http://planktonnet.awi.de>; **D** – *Parvilucifera* sp. sporangium in a deceased dinoflagellate, *Triplos macroceros*, from the North Sea; **E** – *Amoebophrya* sp. in the dinoflagellate *Triplos fusus* from the North Sea. Arrows show extreme points of parasite. All scale bars: 50 µm.

Species of the genus *Paradinium* proliferate as a plasmodium in the tissue of planktonic copepods and produce a sporangium that stays attached for a while externally to the anal pore of the host (Chatton 1910a). Originally thought to be a dinoflagellate (Chatton 1910a, 1920), it has recently been shown, based on molecular phylogeny, to form its own clade within the Rhizaria (Skovgaard and Daugbjerg 2008).

Stramenopiles (Heterokonta)

The Chromalveolate groups Stramenopiles and Alveolate are particularly well represented among protistan parasites of marine plankton, and some of the major alveolate groups, such as Apicomplexa, Perkinsozoa, and the syndinean dinoflagellates, consist exclusively of parasites and are common in the marine plankton. The stramenopile fungi are widespread especially in freshwater habitats (Dick 2001) and are recognized as important degraders of freshwater phytoplankton (Kagami *et al.* 2007). Parasitic stramenopiles are less frequently reported from the marine environment. Many taxa are known only from clone library studies and, while some of these may be parasitic, they are generally assumed to be free-living phagotrophs (Massana *et al.* 2004). The enigmatic species *Solenicola setigera*, which is the first identified member of the marine stramenopile clade MAST-3 (Gómez 2007), appears to be an ectoparasite on the diatom *Leptocylindrus mediterraneus*. However, *S. setigera* has so far only been found on empty frustules and its parasitic nature is thus questionable (Gómez *et al.* 2011). Nevertheless, a few well-documented cases exist on coastal phytoplankton being infected by stramenopiles, such as the Peronosporomycetes *Lagenisma* (Fig. 1B–C, Drebes 1968) and *Ectrogella* (Sparrow 1960), but knowledge of their impact on marine phytoplankton populations is scarce. *Lagenisma* is an intracellular parasite of large planktonic diatoms. *Ectrogella* is a multi-species genus of parasites of primarily freshwater diatoms (Sparrow 1960), but some species are marine, and among these *E. perforans* infects planktonic and epiphytic diatoms in marine and brackish waters (Sparrow 1960).

Another stramenopile genus, *Pirsonia*, is a cluster of species that are parasites of marine diatoms. *Pirsonia* attaches to a host cell and produces a pseudopodium that enters the diatom frustule and phagocytizes the entire host protoplasm (Schnepf *et al.* 1990). Corresponding feeding strategies are found in the little studied parasites *Victoriniella* (Kühn 1997b) and *Palisporomonas* (de Saedeleer 1946). Their taxonomic position remains unclear, but they are functionally related to *Lagenisma* and *Pirsonia* in the sense that these parasites are all potentially important degraders of centric diatoms too large to be grazed by many copepods (Kühn 1997b).

Dinozoa – Dinophyceae and Blastodiniales

Parasitic life modes are common among dinoflagellates, and the species traditionally classified among the

Blastodinales are all parasites (Fensome *et al.* 1993, Coats 1999). Many members of Dinophyceae and Blastodinales are parasites of marine plankton. Marine diatoms are commonly infected with *Paulsenella* spp. that suck out the diatom cell content through myzocytosis (Paulsen 1911, Drebes and Schnepf 1988) and *Paulsenella* spp. is capable of almost eliminating a diatom population (Drebes and Schnepf 1988).

Species of the genera *Duboscquodinium*, *Tintinnophagus*, and *Duboscquella* are all parasites of tintinnid ciliates (Cachon 1964, Coats *et al.* 2010). These dinophycean parasites of tintinnids are typically lethal to their hosts and appear to be widespread and common in the marine plankton.

Oodinium spp. are ectoparasites on various plankton organisms, such as appendicularians (Chatton 1912), chaetognates (McLean and Nielsen 1989), and ctenophores (Mills and McLean 1991). The occurrence of *Oodinium* spp. has been reported in several studies but more or less coincidentally. The same applies to the morphologically similar *Apodinium* spp., ectoparasites on appendicularians (Cachon and Cachon 1973). Both *Oodinium* and *Apodinium* are members of Blastodinales that is today considered a heterogeneous (and paraphyletic) group of core dinoflagellates (Saldarriaga *et al.* 2004, Skovgaard *et al.* 2007, Gómez *et al.* 2009). The original type genus of Blastodinales, *Blastodinium*, comprises photosynthetic parasites that live in gut of marine planktonic copepods, particularly in warm temperate to tropical waters (Chatton 1920, Skovgaard *et al.* 2012). Blastodinales also includes the peculiar genus *Haplozoon* (Fig. 2A) and ectoparasites of copepod eggs, namely *Dissodinium* and *Chytriodinium* (Cachon and Cachon 1968a, Drebes 1969). Copepod eggs are also exploited by a couple of rarely reported dinophycean parasites, *Syltodinium* and *Schizochytriodinium* (Drebes 1988, Elbrächter 1988).

Dinozoa – Syndiniales

The Syndiniales (or Syndinea, Cavalier-Smith 1993) are an assembly of parasitic dinoflagellates that are both genetically and morphologically different from the dinophycean dinoflagellates (Fensome *et al.* 1993, Guillou *et al.* 2008). Recent analyses of environmental marine rDNA sequences have revealed an extensive diversity of ribotypes related to Syndiniales (López-García *et al.* 2001, Moon-van der Staay *et al.* 2001). Phylogenetic analyses consistently place these alleged Syndinean sequences in two main clades (Marine Alveolate Groups I and II) and, in some analyses, 3–5 ad-

ditional minor clades (Richards and Bass 2005, Guillou *et al.* 2008).

Based on molecular phylogeny, the syndineans *Amoebophrya* and *Syndinium* are established members of Marine Alveolate Group II (group II and IV, respectively, according to the scheme of Guillou *et al.* 2008). *Amoebophrya* spp. are parasites of various plankton organisms (Cachon 1964) and may play important roles in the dynamics of bloom-forming dinoflagellates (Park *et al.* 2004, Chambouvet *et al.* 2008). Other *Amoebophrya* species are found in radiolarians, ciliates, and as hyperparasite in *Oodinium* (Cachon 1964, Fig. 2B–C). *Syndinium* spp. (Fig. 2D–H) are parasitoids that infest and devour several species of calanoid copepods (Fig. 2F–H, Chatton 1910b, Skovgaard *et al.* 2005) and, in addition, the Syndinean genera *Merodinium*, *Solenodinium*, and *Keppenodinium* infect radiolarians and phaeodarians (Hollande *et al.* 1953, Hovasse and Brown 1953, Hollande and Enjume 1955). The latter three genera have received almost no scientific attention for decades and rDNA sequences are currently not available for any of the known syndineans infecting radiolarians or phaeodarians.

Until now, only two genera are confirmed members of the Marine Alveolate Group I clade, which is otherwise comprised by environmental rDNA sequences. *Ichthyodinium* is parasite of pelagic eggs of numerous species of marine fish (Hollande and Cachon 1952, Meneses *et al.* 2003, Skovgaard *et al.* 2009). The other genus, *Euduboscquella*, comprises parasites of ciliates (Harada *et al.* 2007, Coats *et al.* 2012) and dinoflagellates (Cachon 1964). In Group I, a number of sequences have been identified from protists associated with radiolarians and phaeodarians (Dolven *et al.* 2007) and it is likely that these are parasites. Indeed, a recently observed probable parasite of a radiolarian had similarity with *Euduboscquella* (Suzuki *et al.* 2009). Thus, it is possible that some of these Marine Alveolate Group I sequences correspond to syndinean parasites from which no rDNA sequences are yet known.

Dinozoa – Perkinsidae

The Perkinsidae are primarily known for the genus *Perkinsus* which are endocellular parasites of oysters (Siddall *et al.* 1997). However, a parasite of dinoflagellates, *Parvilucifera infectans*, was found to be affiliated with the perkinsids (Norén *et al.* 1999, Fig. 1D). Recently, two additional *Parvilucifera* species were identified (Figueroa *et al.* 2008, Hoppenrath and Leander 2009), illustrating that species diversity in this group

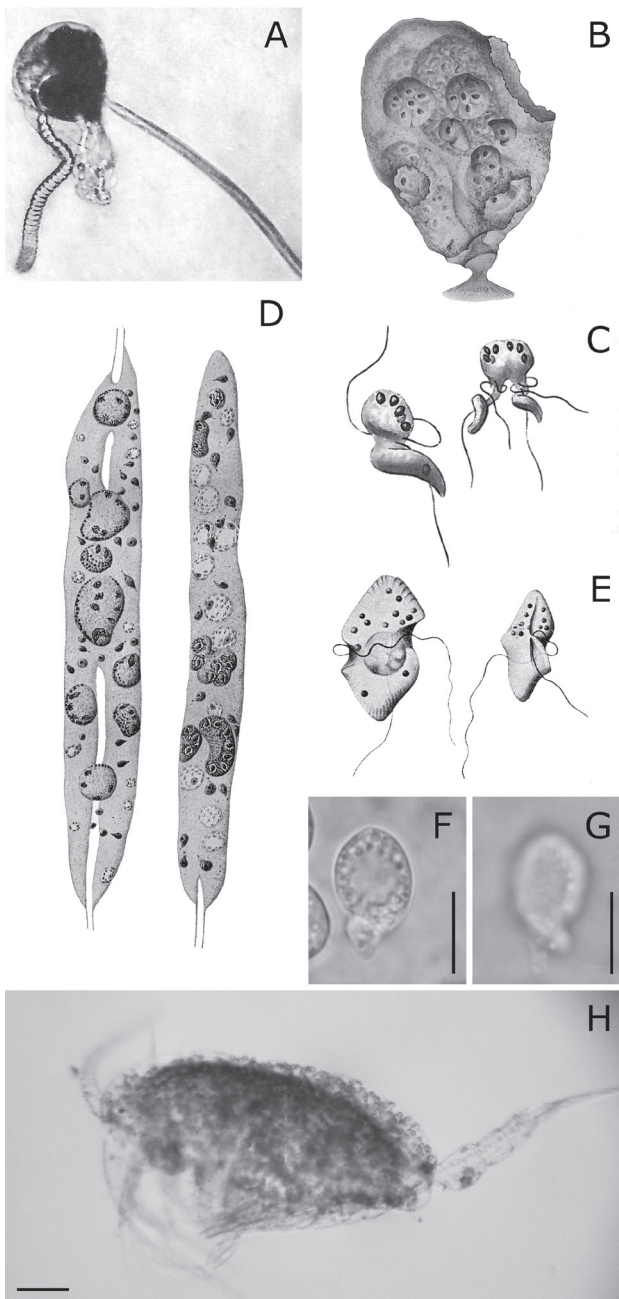


Fig. 2A–H. Protistan parasites of marine zooplankton. **A** – the dinoflagellate *Haplozoon inerme* (bottom left) parasitizing *Appendicularia sicala* (after Cachon 1964); **B, C** – hyperparasitic *Amobophrya grassi* in *Oodinium poucheti*, an ectoparasites on *Oikopleura* (after Cachon 1964); **B** – several early-stage parasites inside the host; **C** – macrospore (left) and dividing microspores (right) of *A. grassi*; **D, E** – the syndinean dinoflagellate *Syndinium bogerti* in the acantharian *Amphilonche* sp. (after Hollande and Enjume 1955); **D** – multinuclear parasites inside the host; **E** – relaxed parasite macrospore (left) and microspore (right); **F–H** – *Syndinium*-like parasite in the copepod *Clausocalanus* sp. from the NW Mediterranean Sea; **F, G** – dinosporos originating from the infected host in **H**. Scale bars: 10 μ m; **H** – recently diseased host filled with live dinosporos. Scale bar: 100 μ m.

is probably underestimated. Studies of environmental DNA sequences have supported this by identifying a large amount of assumed hidden perkinsid taxa primarily from freshwater environments but also from the Mid-Atlantic Ridge hydrothermal area (Lefèvre *et al.* 2008, Bråte *et al.* 2010).

Ciliophora

The ciliates are an overwhelmingly diverse group of protists in which parasitic life styles are common (e.g. Bradbury 1994), but comparably few ciliate species are known to infect marine plankton organisms. A couple of remarkable exceptions, which may exert profound effects on their host populations, are *Collinia* and *Pseudocollinia* infecting euphausiids (Gómez-Gutiérrez *et al.* 2006, Gómez-Gutiérrez *et al.* 2012). *Collinia* and *Pseudocollinia* are parasitoids that may cause mass mortality in host populations (Gómez-Gutiérrez *et al.* 2003). Also live copepods may be infested with ciliates. Two ciliate species, *Uronema rabaudi* and *Perezella pelagica*, were described from live specimens of *Acartia clausi* and *Pseudocalanus elongatus*, and *Paracalanus parvus*, respectively (Cépède 1910). Similar endoparasitic ciliates have been found in the calanoid copepods *Calanus finmarchicus* and *Pseudocalanus* (Apstein 1911), suggesting that these parasites may be widespread even though they have now gone unnoticed for decades. An apostome ciliate, *Metaphrya sagittae*, occupies the coelom of chaetognates and appears to be very common in a range of species (Ikeda 1917, Weinstein 1973). It has been found in most of the world's oceans (Weinstein 1973), but recent records of the species are scarce. Ciliates of the genus *Trichodina*, which comprises common parasites on marine and freshwater fish, exist as ectoparasites on ctenophores (Estes *et al.* 1997). *Trichodina* spp. are also found on copepods, but have so far only been found in freshwater (Green and Shiel 2000).

Ellobiopsidae

Several species of the enigmatic group Ellobiopsidae are ectoparasites on planktonic crustaceans. The genus *Ellobiopsis* is restricted to copepods, whereas *Thalassomyces* spp. infect larger crustaceans, including euphausiids and mysids (Boschma 1959, Vader 1973). The stalk of the parasite penetrates the host exoskeleton and nourishes itself from tissue or body fluids of the host. *Ellobiopsis*-like protrusions have also been found on freshwater copepods, but the exact identity of these is controversial (Rayner and King 1986, Bridgeman *et al.* 2000, Skovgaard 2004).

Apicomplexa

Apicomplexans are a successful group of parasitic protists that infect a wide range of organisms, including invertebrates of the marine plankton (Théodoridès 1989). For example, gregarine apicomplexans commonly inhabit the intestine of chaetognates (Leuckart 1861, Weinstein 1973, Théodoridès 1989). Large fractions of Arctic krill, *Euphausia superba*, may also be infected with the gregarine *Cephaloidophora pacifica* (Takahashi *et al.* 2008) just as sporadic reports have noted parasitic gregarines in copepods. The first report was that of *Paraophiodina haeckeli* in *Sapphirina* spp. in the late 19th century (summarized by Théodoridès and Desportes 1972) and this genus has subsequently been found in other copepod species (Apstein 1911, Levine 1977). Other observations include *P. copilia* in *Copilia vitrea* (Rose 1933) and *Cephaloidophora petiti* in *Candacia aethiopica* (Gobillard 1964). Furthermore, parasitic gregarines exist in planktonic polychaetes, amphipods, hyperiids, mysids, mollusks, and tunicates (Théodoridès 1989), but also in these cases information on ecology and impact of parasites is virtually non-existing.

Excavata – Euglenozoa

In contrast to the freshwater environments in which many euglenid species are parasites of plankton organisms (Michajłow 1972), only few parasitic euglenozoa are known from marine plankton. *Rhynchopus coscinodiscivorus* (Diplonemea) has been described as a parasite of marine diatoms (Schnepf 1994). This species may be a facultative parasite, considering that other species of *Rhynchopus* are free-living phagotrophs (Roy *et al.* 2007). A few accounts also exist on the infection of chaetognates with the kinetoplastid *Trypanophis sagittae* (Hovasse 1924, Rose and Hamon 1950). Drebes (1974) reported on an unidentified euglenid infecting eggs of the copepods *Temora* and *Acartia*.

UNRECOGNIZED PARASITE DIVERSITY

Many parasites of marine plankton are poorly investigated and the taxonomic affiliation of several parasite species is uncertain. In a Norwegian fjord, for example, the copepods *Calanus* spp. were found parasitized by an organism producing yellow hypha-like structures (Torgersen *et al.* 2002). It was not possible to identify it solely based on morphology and no genetic information

is yet available. Another parasite of copepods, tentatively named red plasmodial parasite, was shown through molecular phylogeny to be a member of Marine Alveolate Group I (Skovgaard and Daugbjerg 2008), but has yet not been formally described. This parasite was also observed by Jepps (1937).

Even among the formally described protistan parasites, several species have been observed only one single or a few times following their original description and then often many decades ago. This is the case for e.g. the blastodinians *Syltadinium* and *Schizochytriodinium* (infecting copepod eggs, Drebes 1988, Elbrächter 1988), *Actinodinium* (in copepods, Chatton and Hovasse 1937), *Cachonella* (on siphonophores, Rose and Cachon 1951), and *Myxodinium* (in a prasinophyte, Cachon *et al.* 1969), and also for such dinophyceans as *Filodinium* (on appendicularians, Cachon and Cachon 1968b). This also applies to several of the (often abundant) parasites of diatoms that have been reported by few researchers apart from their original authors (Schnepf *et al.* 1978, Schnepf *et al.* 1990, Kühn *et al.* 1996, Schweikert and Schnepf 1996). In addition, certain species of the better-known genera *Amoebophrya*, *Duboscquella* and *Syndinium* have completely avoided the attention of scientists, e.g. *A. grassei* in *Oodinium* (Fig. 2A), *A. acanthometrae* in a radiolarian, *D. melo* in the free-living dinoflagellate *Noctiluca* (Cachon 1964), and *S. oikopleurae* in an appendicularian (Hollande 1974). In the case of *Amoebophrya*, only few species have been described, but the genus represents a considerable genetic diversity which does point towards the existence of numerous species within the genus (Salomon *et al.* 2003, Kim *et al.* 2008) and the same may be the case for other syndinean genera (Gómez 2014). Likewise, the genetic and morphological diversity within the genus *Blastodinium* suggest that the number of actual species is larger than currently acknowledged (Skovgaard *et al.* 2012).

Hence, taxonomy and species diversity of marine plankton parasites is incompletely explored and it is plausible that the number of protistan species that are parasites of marine plankton is considerably underestimated. This postulation is in line with research having revealed large numbers of sequences originating from unknown taxa affiliated with parasitic groups, such as syndineans (López-García *et al.* 2001, Guillou *et al.* 2008) and perkinsids (Lefèvre *et al.* 2008). Given the fact that DNA sequences are yet not available for the majority of known syndinean parasites, it is tempting to suggest that at least some of the environmental se-

quences that fall within the marine alveolate clades are, in fact, syndinean parasites. There appears to be a particular variety of environmental sequences (i.e. potential parasites) associated with radiolarians (Gast 2006, Dolven *et al.* 2007). However, some of these cluster with photosynthetic dinoflagellates and one should keep in mind that radiolarians frequently host photosynthetic symbionts (Anderson 2014). Furthermore, not all DNA sequences obtainable may necessarily correspond to a valid species, since artifact sequences do occur in large-scale sequencing studies (Bachy *et al.* 2013).

EFFECTS AND IMPACT OF PARASITES IN MARINE PLANKTON

The effect of protistan parasites in the marine plankton is very variable dependent on parasite species. In the protist hosts, parasites typically have characters of parasitoids, i.e. the host cell is killed by the parasite, which is in turn depending on the host for completion of its life cycle. Parasitoids also occur in multicellular zooplankton, such as *Syndinium* infecting copepods or *Collinia* infecting euphasids. However, not all protistan parasites in zooplankton are lethal to their hosts. Infection with ellobiopsids, e.g., may not be detrimental to their hosts, but induces sterility in female copepods (Albaina and Irigoien 2006). *Blastodinium* appears to stay relative harmless inside the host's gut, but it does affect the host's fitness (Skovgaard 2005) and it causes sterility in infected females (Chatton 1920). Similar to the parasitic castrators, parasites infecting zooplankton eggs, such as *Dissodinium* and *Chytriodinium*, are not destructive for the adult host, but may have significant effects on host recruitment.

While observations on dramatic effects of parasites on single phytoplankton cells or cell cultures are ample (e.g. Drebes 1966, Kühn 1998), few investigations have aimed at determining the impact of such pathogens in marine phytoplankton populations. Prevalence data are available in a few examples and, even though detailed information on parasite growth and generation time does not always exist, prevalence itself gives an indication of parasite impact. For example, large-scale *Pirsonia* spp. infections have recurrently been found in several diatom species in coastal waters (Schnepf *et al.* 1990, Kühn *et al.* 1996, Tillmann *et al.* 1999), giving good reasons to assume that these parasites play important roles in regulating host populations. It has like-

wise been justified that parasitism by *Cryothecomonas* at times may successfully compete with zooplankton in controlling energy flow and food web dynamics (Tillmann *et al.* 1999). Particular interest has arisen with the fact that many dinoflagellate species responsible for toxic algal blooms are susceptible to infection by the parasitoid syndinean *Amoebophrya*, opening potentials for combatting these blooms through biological control (Taylor 1968). *Amoebophrya* does reach high infection prevalence in cultures with the capability to wipe out some host species (Coats and Park 2002). This is to some extent supported by field investigations estimating that *Amoebophrya* was capable of inducing 0-5% mortality per day among its dinoflagellate host populations in coastal waters, and up to 54% per day in localized epidemics (Coats *et al.* 1996). Gisselson *et al.* (2002) estimated mortality rates in *Dinophysis norvegica* of max. 2% per day due to *Amoebophrya* infections and referred to unpublished data showing 20% of *Dinophysis* infected by *Parvilucifera infectans* in the Baltic Sea. Thus, as reviewed by Park *et al.* (2004), these parasites can have significant impacts on host bloom dynamics. This has also been demonstrated more recently by Chambouvet *et al.* (2008) showing that a given dinoflagellate host species was infected by a genetically distinct *Amoebophrya* clade year after year and that a decline in dinoflagellate populations correlated with release of free-swimming parasite spores.

Also microzooplankton populations are regulated by parasites. Species of the genera *Duboscquodinium*, *Duboscquella*, and *Euduboscquella* are distributed worldwide and notable infection frequencies are often observed in ciliate population (Coats and Bachvaroff 2013). The syndinean *Euduboscquella cachoni* was estimated to remove 7-24% of its ciliate host population biomass per day in Chesapeake Bay through parasite-induced mortality (Coats and Heisler 1989). Such mortality rates indicate that parasite-induced mortality of the ciliates is comparable to predation pressure by larger zooplankton grazers. In general, data on the impact of parasitic protists on natural zooplankton populations rely on field observations of parasite prevalence with only little information available from culture work. In this manner, *Syndinium* has been estimated to – in peak periods – be prevalent enough to affect copepod populations at a magnitude similar to that of predators (Ianora *et al.* 1987, Skovgaard and Saiz 2006). *Syndinium* is a cosmopolitan genus and a study in Sydney harbor concluded parasite-induced mortality of the copepod *Paracalanus indicus* to be about 1/3 of total

mortality (Kimmerer and McKinnon 1990). Otherwise, reports on high mortalities of zooplankton due to protistan parasites are infrequent, but an unusual excessive number of euphasiid carcasses near the ocean floor in the Pacific Ocean has revealed that the parasitoid ciliate *Collinia* is able to cause mass mortalities of euphasiids (Gómez-Gutiérrez *et al.* 2003). Earlier studies have shown prevalence as high as 64–98% in similar host-parasite associations (Capriulo *et al.* 1991). Intuitively, such high prevalence of a parasitoid must have significant consequences for the host population.

The effects of non-lethal zooplankton parasites are less evident than the drastic effects of parasitoids on host individuals. Nevertheless, adverse effects on fecundity and recruitment may have profound consequences at the population level. In a study of Western Mediterranean zooplankton it was found that the parasitic blastodinium *Blastodinium* spp. were responsible for an impairment of reproductive rates of up to 0.16 and 0.03 per day for the copepods *Oncaea* cf. *scottodicalloi* and *Paracalanus parvus*, respectively (Skovgaard and Saiz 2006). Also in the Eastern Mediterranean Sea *Blastodinium* infections are common and prevalence up to 2–51% were found in different taxonomic groups of copepods (Alves-de-Souza *et al.* 2011), suggesting that these parasites may markedly suppress copepod production. A reduction in fecundity of about 7% for population of the copepod *Calanus helgolandicus* in the Bay of Biscay was assigned to parasitism by *Ellobiopsis* sp. (Albaina and Irigoien 2006).

As outlined above, parasitism in the marine plankton is all but a rarity and parasites are common in both zooplankton and phytoplankton. Yet there are few accounts on the prevalence and role of such parasites. This may be a result of the great diversity of the nature of parasites, making it difficult to encompass them all in standard plankton studies. The vast variety and abundance of parasitic protists demonstrate that this category of organisms is an important element of the marine plankton and there is good reasons to expect that the prevalence – and thereby the ecological significance – of parasites in the marine plankton is overlooked to a large extent. Thus, ignoring these parasites in ecosystem studies will bias the true picture of biological interactions and energy flow in the system. It has been argued that ecosystem model studies should include parasites (Lafferty *et al.* 2008), an opinion that is also valid for marine plankton ecosystems. Theoretically, this should not be problematic, but in the case of the marine plankton a couple of obstacles exist:

1) many parasitic protists are either not described or poorly known and 2) ecosystem research teams often lack the incorporation of skills needed for identification and quantification of parasites.

Most studies on the impact of parasites in marine plankton have been based on detecting parasites using traditional light microscopy, which most likely underestimates true parasite prevalence (Skovgaard and Saiz 2006). Important steps for future research will, therefore, be to gain more knowledge about these parasitic protists and to develop improved methodologies for their quantification. Specific staining of parasites (Alves-de-Souza *et al.* 2011) may turn out useful to quantify more efficiently and accurately the occurrence of parasites in planktonic organisms. It will be of importance, however, that such methodologies are applicable to a larger number of host organisms, and it should be possible to screen for parasites in preserved samples in order for the methods to be of broader use in ecological studies.

Acknowledgements: This work was supported through the project IMPAQ – IMProvement of AQUaculture high quality fish fry production (J. no. 10-093522), funded by the Danish Council for Strategic Research.

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Received on 2nd June, 2013; revised on 4th July, 2013; accepted on 7th July, 2013